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SPECIAL ISSUE PAPER

Zoonotic diseases: New directions in human–animal pathology

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Abstract

Zoonotic diseases—human diseases of animal origin—represent one of the world's greatest health challenges, both today and in the past. Since the Neolithic, zoonotic diseases have been one of the major factors shaping and influencing human adaptation. Archaeology is ideally situated to provide the long view on human–animal–pathogen relationships through combining cultural, environmental and biological datasets, yet long-term studies of linked human and animal records have often been overlooked and undertheorized. The seven papers in this special issue “Zoonotic diseases: New directions in human–animal pathology” cover a range of diseases caused by bacterial, viral, and parasitic pathogens, from case studies drawn from across Europe, Asia, Africa and the Americas. They speak to the diversity of human–animal–environment interactions that shaped disease emergence and transmission. They also review methodological advancements relating to disease identification and interpretation and discuss interdisciplinary approaches to effectively investigate these complex processes in the past. This introduction highlights their key themes and outcomes and identifies research priorities moving forward.

KEYWORDS

ancient DNA, demography, epidemiology, One Health, palaeopathology, pathogens, taphonomy, zoonoses

1 | INTRODUCTION

Zoonotic diseases—human diseases of animal origin—represent one of the world's greatest health challenges, both today and in the past. Since the Neolithic, zoonotic diseases have been one of the major factors shaping and influencing human adaptation (Stone, 2020). The ongoing interaction between animals and humans with regard to pathogens is profoundly visible in the current global health and economic consequences of the Covid-19 pandemic, stemming from the spillover of an animal-borne pathogen (SARS-CoV-2) in 2019 into human communities in Wuhan, China (Andersen et al., 2020; UNEP and ILRO, 2020). The Covid-19 pandemic is only the latest of a series of emerging zoonotic diseases to impact the world in recent decades, such as severe acute respiratory syndrome (SARS), Middle East

respiratory syndrome (MERS), Ebola and Zika virus (UNEP and ILRO, 2020). In the contemporary context, a number of changing human–animal–environment relationships are understood to be major drivers of zoonotic disease emergence (Hassell et al., 2017; Jones et al., 2013; Plowright et al., 2017).

The first epidemiological transition occurred at the beginning of the Neolithic approximately 10 000 years ago, and it is here that the domestication of plants and animals set the stage for the intensification of human–animal relationships, which stimulated an unprecedented increase in the number, type and severity of diseases spread to humans (Larsen, 2018; McMichael, 2004; Mitchell, 2003). Long-term studies of combined human and animal records across this and other transitions have often been overlooked and often undertheorized. Archaeological records are ideally situated to generate key

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insights into the long-term trajectories of shared diseases in humans and animals and the relationships that enabled the transmissions of infections. These changing human–animal relationships through time have had important consequences on disease ecology and the incidence of mutually shared infectious diseases. The epidemiology of these infectious diseases was shaped by diverse biological, environmental and cultural variables. Their study can shed important light upon the health implications of infectious diseases for past humans and animals in terms of the health of populations, but also in terms of social dynamics, economic practices and losses, and living conditions.

The seven papers in this special issue “Zoonotic diseases: New directions in human–animal pathology” cover a range of diseases caused by bacterial, viral, and parasitic pathogens, from case studies drawn from across Europe, Asia, Africa and the Americas (Beltrame et al., 2019; Bendrey et al., 2020; Boschin, 2020; Lawler et al., 2020; Ledger & Mitchell, 2019; Seetah et al., 2020; Wooding et al., 2019). They speak to the diversity of human–animal–environment interactions that shape disease emergence and transmission. They also review methodological advancements relating to disease identification and interpretation, and discuss interdisciplinary approaches to effectively investigate these complex processes in the past. Here, we introduce these papers, highlight key outcomes and themes from them and identify research priorities moving forward (see Box 1).

Box 1. Summary of key research priorities outlined in this special issue for the investigation of past zoonoses (see text for details)

1. Investigate human and animal skeletal evidence together from study sites and regions and in particular such examples where articulating animal skeletons are available.
2. Further develop understanding of the macroscopic pathological expression of zoonotic diseases in both human and animal skeletons.
3. Differential diagnoses should entertain the potential for multiple pathogens present.
4. Differential diagnoses should consider soil microbiology when discussing identifications of disease made by DNA analyses.
5. Extend palaeoparasitological studies for greater global coverage, filling in regional “gaps” and developing more consistent coverage.
6. Greater focus on wildlife sources of infection for domestic animal and human health risks in past ecosystems.
7. Develop genetic studies on ancient parasite DNA to investigate evolutionary trajectories and phylogenies.
8. Foetal and neonatal zooarchaeological remains should be considered as potential indicators of abortifacient pathogens.

9. Conceptualization of zoonotic disease needs to be able to capture the component factors influencing infections to consider in holistic and integrated analyses.
10. Epidemiological and anthropological contextualization of archaeological evidence for zoonoses should be focused to investigate the factors promoting disease emergence.
11. Epidemiological modeling of human–animal–environment relationships should be used to generate hypotheses about zoonosis emergence drivers and target investigations of the archaeological record.
12. Understanding of past zoonoses should be used to inform the present and future.

Both human and animal palaeopathology can deliver essential and connected evidence relating to past health and human–animal interactions, yet the potential of this has not yet been fully realized. The study of Wooding et al. (2019) stresses the importance of investigating human and animal skeletal evidence together from study sites and regions and in particular such examples where articulating animal skeletons are available (Box 1, *Priority 1*). Their study reviews human and animal samples from the same site (Wetwang Slack, UK) to evaluate palaeopathological evidence for zoonotic diseases and specifically bovine tuberculosis (bTB). In a similar vein, Bendrey et al. (2020) review evidence and methods for identifying brucellosis in the past, a disease caused by bacteria of the genus *Brucella*, focusing on osteological markers in both animals and humans, with data generated from biomolecular, epidemiological and historical approaches. Brucellosis is the most common bacterial zoonosis in the world today, yet it is remarkably rare in the archaeological record.

The challenges of differential diagnosis of some infectious diseases via macroscopic examination of skeletal material are clearly presented in this special issue. Wooding et al. (2019) argue that for tuberculosis, the inability to separate the bovine (*Mycobacterium bovis*) and human (*Mycobacterium tuberculosis*) strains has led to the underestimation of the former (bTB) in both past and present populations. Similarly, the variability in pathological expression of brucellosis in the human body means that this disease is also under-recorded in both past and present populations (Bendrey et al., 2020). When we consider macroscopic assessment of faunal remains, this situation becomes even more challenging, as the majority of archaeological animal remains are fragmentary rather than found in articulation and there is less knowledge for these diseases in animal bodies relative to the comparatively well-studied humans (Bartosiewicz, 2008; Bartosiewicz & Gál, 2013). Focus should be placed on further developing understanding of the macroscopic pathological expression of these diseases in human and animal skeletons (Bendrey et al., 2020; Wooding et al., 2019; *Priority 2*). Differential diagnoses should also

entertain the potential for multiple pathogens present (*Priority 3*), and not just be guided by targeted assumptions, given their potential to contribute to disease in interacting ways (Lawler et al., 2020). Lawler et al. (2020) further propose that soil microbiology should also be framed within consideration of differential diagnosis when discussing identifications of disease made by DNA analyses (*Priority 4*).

Two papers in this special issue examine zoonotic parasites and draw on their life cycles and host requirements (Beltrame et al., 2019; Ledger & Mitchell, 2019). Ledger and Mitchell (2019) review the published evidence for zoonotic endoparasites in the global archaeological record and combine this with studies on molecular phylogenetic reconstructions and modern epidemiological data to provide insights on the evolutionary, cultural and ecological factors in their emergence. The review offers a very useful collation of published palaeoparasitological evidence from human pelvic soil contexts and mummified remains (to ensure linkage to a human host) from all global regions (see Ledger & Mitchell, 2019; tab. 2–6). Ledger and Mitchell (2019) acknowledge the restricted regional and temporal focus of much research and identify the need for extension of palaeoparasitological studies for greater global coverage (*Priority 5*). Also addressing parasites, Beltrame et al. (2019) investigate samples from wild felid (puma or jaguar) coprolites from northeast Patagonia, Argentina, and explore the potential diseases that might have been present in these populations, including some with zoonotic potential. Wildlife sources of infection are important sources of domestic animal and human health risk (Jones et al., 2013; Perri et al., 2018) and their investigation should be developed in archaeological research (*Priority 6*).

Ancient DNA analyses in particular demonstrate the potential to explore the evolution of pathogens and also the ancient spatial networks that enabled disease transmission and spread (e.g., Bos et al., 2019; Hershkovitz et al., 2015; Marciniak & Poinar, 2018). A number of the papers in this special issue discuss the investigation of zoonotic pathogens through ancient DNA (Bendrey et al., 2020; Lawler et al., 2020; Ledger & Mitchell, 2019; Wooding et al., 2019). In a contribution to the interpretation of high-throughput DNA sequencing of osteological samples and the discrimination of soil-derived relatives of the pathogens of interest (Warinner et al., 2017), Lawler et al. (2020) provide a detailed assessment of potential processes of post-depositional microbial contamination. They discuss soil biology and microbial movement, with a particular focus on the identification of tuberculosis and soil-related contamination. Considerations of taphonomy and preservation may also impact recovery of pathogen DNA, for example, with the outer cell wall of mycobacterial species thought to enable better preservation than that of *Brucella* spp. and thus impact relative identification rates (Bendrey et al., 2020; Wooding et al., 2019; and references therein). Development of DNA work on archaeological parasites is also an area identified in need of future development (*Priority 7*), to investigate evolutionary trajectories and phylogenies (Ledger & Mitchell, 2019).

Several papers employ palaeodemographic information to provide insights on past disease experience. In a detailed assessment of caprine mortality profiles from Neolithic northern Adriatic sites,

Boschin (2020) considers the foetal and neonatal remains as indicators of animal disease (*Priority 8*). A range of pathogens cause abortions in livestock (see also Bendrey et al., 2020, tab. S1), and although it is challenging to demonstrate the role of infectious disease in such assemblages, the presence of these remains as an archaeological signature may contribute to developing multiproxy strands of indirect evidence and helping to target further genetic investigations to confirm pathogen presence (Bendrey et al., 2020; Boschin, 2020). The demographic structure of caprine herds is also discussed by Bendrey et al. (2020) from the point of view of understanding the impact of herd management decisions (i.e., decisions over age and sex composition of herds), on the potential for *Brucella melitensis* to have become endemic within Early Neolithic goat herds from the Zagros Mountains of Iran, based upon understanding of the present-day pathogen ecology (see also Fournié et al., 2017).

The conceptualization of past zoonotic diseases fundamentally shapes the ways in which we approach and interrogate the archaeological record. It needs to be able to ensure that the component factors influencing infections are considered in holistic and integrated analyses (*Priority 9*). A number of authors advocate the use of a “One Health” approach that explicitly links the health of people, animals and environments (Bendrey et al., 2020; Seetah et al., 2020). Closely aligned with biocultural approaches (Leatherman & Goodman, 2020; McElroy, 1990), One Health considers health in its fullest context and also advocates an explicitly interdisciplinary approach, moving away from siloed disciplinary approaches (Johnson-Walker & Kaneene, 2018; Lebov et al., 2017). The study of zoonoses is a clear case that benefits from this approach given the ways these diseases function. We should also be careful not to fall into anthropocentric approaches and ignore the role of humans in disease networks, either as agents who shape the relationships or as the sources of infection (e.g., Ledger & Mitchell, 2019). While animals have been the source of many infectious diseases by spillover into human populations (Plowright et al., 2017; Woolhouse & Gowtage-Sequeria, 2005), pathogen flow can and does move in the opposite direction, and we must consider infections that pass from humans to animals, known as reverse zoonoses or zooanthroponoses (Messenger et al., 2014), and ongoing cycles of spillover and spillback. The One Health approach helps to frame the full potential complexity of past disease relationships.

Although investigations of past zoonoses have tended to focus on palaeopathological and biomolecular analyses, a complementary approach is provided by palaeoepidemiological modeling, which is delivering new understanding of the factors influencing disease emergence and transmission (e.g., Fournié et al., 2017; King et al., 2017). Work should further develop the epidemiological and anthropological contextualization of diseases identified in the past to investigate the factors promoting zoonotic emergence (Bendrey et al., 2020; *Priority 10*). Seetah et al. (2020) present an archaeo-historic modeling framework using deep learning tools (data-driven neural network technology) for the analysis of Rift Valley fever (a bunyavirus transmitted by arthropod vectors). Their approach proposes to integrate data on climate, landscape archaeology, historical evidence

and human behavior to produce a predictive model for Rift Valley fever outbreaks, promising new ways to assemble and assess data (Priority 9). Epidemiological modeling of human–animal–environmental relationships can be used to generate hypotheses about zoonosis emergence drivers and focus investigations into the archaeological record (Bendrey et al., 2020; Priority 11).

Several papers in this special issue tie into contemporary understanding of zoonoses (Bendrey et al., 2020; Ledger & Mitchell, 2019; Seetah et al., 2020; Wooding et al., 2019). Archaeology is well placed to offer long-term records on biological and social contexts of disease (Bendrey & Fournié, 2020; Marciniak, 2016; Roberts, 2016). Understanding of the past should be used to inform the present and future (Priority 12). Seetah et al. (2020) stress the chronological context of disease, and their approach is strongly directed at evaluating the archaeo-historic record to contribute to prediction of future outbreaks of Rift Valley fever. This long view context is useful for understanding of disease emergence, impact, recovery and hopefully prevention (DeWitte, 2016; Hughes et al., 2010; UNEP and ILRO, 2020). It is also useful for exploring how people react to and process knowledge of zoonotic disease. Indeed, archaeological knowledge may have the potential to help communities process information on contemporary health challenges more effectively. By communicating understanding about temporally distant experiences, it can avoid portraying risks as imminent, which can lead to defensive responses (Bendrey & Fournié, 2020).

In conclusion, what is clear as we discuss zoonoses is that the complexity of studying and understanding their past ecology and archaeological expression demands an interdisciplinary foundation. The papers in this special issue all contribute different perspectives on this complex world. They articulate a series of original and significant contributions to understanding past zoonoses from which we can draw a number of directions to inform an agenda that will reach across diseases, pathogens and contexts (Box 1). This agenda outlines a number of methodological and theoretical directions, in particular emphasizing integrated interdisciplinary and strongly contextualized approaches.

In a contemporary world deeply challenged by zoonotic disease (UNEP and ILRO, 2020), the value of understanding past disease experience and context comes into focus. It also brings home the understanding that infectious disease is shaped by socio-ecological systems—we need to consider not just biology, but human decisions and actions. Archaeology can provide the long view on past human–animal–pathogen relationships and provide the link between ancient cultural and biological parameters. It can explain, contextualize and inform. It may even be able to help communicate health messaging. The studies in this special issue demonstrate how interdisciplinary research into the past are dealing with this complexity and developing approaches that are innovative, significant and relevant.

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